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ISSN 0038-3872

SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

BULLETIN

Volume 110 Number 1

SMITHSONIAN
JUL 2 0 2011
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BCAS-A110(1) 1–34 (2011) April 2011

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Date of this issue 8 July 2011

♾ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

Bull. Southern California Acad. Sci.
110(1), 2011, pp. 1–16
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Colonization and Persistence of a Southern California Steelhead (*Oncorhynchus mykiss*) Population

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Abstract.—The life history and habitat interactions of southern *Oncorhynchus mykiss* populations have received less attention than their Pacific Northwest counterparts. In this article we create a conceptual model describing the factors affecting *O. mykiss* population dynamics in Topanga Creek, Los Angeles County, California to understand the process that led to extirpation following floods in 1980 and 1983, re-colonization in the late 1990's, and continued persistence. We conclude that key factors influencing population dynamics include life-history variability with both resident and anadromous individuals, population spatial structure connecting Topanga Creek with other watersheds within the metapopulation, exclusive distribution within the mainstem Topanga Creek, high-quality summer and winter rearing habit, and food availability sufficient to maintain growth at high temperatures. Protecting the population in Topanga Creek from future extirpation should include restoration of the lagoon, and preventing changes to the flow regime and water quality.

Introduction

Anadromous steelhead and resident rainbow trout in Topanga Creek belong to the federally endangered Southern California Steelhead Evolutionarily Significant Unit (now Distinct Population Segment [DPS]), as modified in July 2002. *O. mykiss* within Topanga Creek and other watersheds within the DPS are considered as part of the same metapopulation (group of sub-populations with genetic exchange). Steelhead is the term used to denote the anadromous life-history form of rainbow trout (*Oncorhynchus mykiss*). Because both anadromous and resident *O. mykiss* are found within the watershed, the term *O. mykiss* is used in situations where distinguishing juvenile steelhead from resident rainbow trout would be problematic. Preservation of both life-history forms is considered a high priority in the *Southern Steelhead Recovery Plan* (National Marine Fisheries Service 2009). *O. mykiss* stocks throughout California and in southern California in particular have substantially declined; only an estimated 500 adult steelhead remain in the Southern California DPS (National Marine Fisheries Service 2009). This DPS is considered at high risk for extinction as a result of an extirpation from much of their historical range (Boughton et al. 2005, Boughton et al. 2006); resulting in increased susceptibility to loss of genetic diversity and poor population growth rates (McElhany et al 2000).

The role of colonization and intermittent access of anadromous adults is paramount to moderating unnatural alteration of population spatial structure and mitigating the related risk of regional extinctions (Boughton et al. 2006), but is rarely documented. Challenges to colonization of new or historical habitat in southern California include highly variable flow regimes, high water temperatures, and frequent isolation from the Pacific Ocean by sandbars that develop at the mouths of most coastal streams. Few aquatic species are adapted to surviving in such conditions. *O. mykiss*, however, is a highly plastic species in terms of phenotypic and life-history variability, capable of exploiting habitats that would not sustain populations of other salmonids. Despite the contraction of southern California steelhead from their historical range, we believe that a sub-population in Topanga Creek, California has been re-established (i.e., re-colonized) within the last 20 years. Topanga Creek drains a 47 km^2 watershed within Los Angeles County and adjacent to the city of Los Angeles. Research has been ongoing for nearly a decade within a study reach that extends from the ocean upstream to the northern boundary of Topanga State Park at river kilometer (rkm) 6, which is just below the village of Topanga. Our objectives were to synthesize nine years of research on *O. mykiss* in Topanga Creek (Dagit and Reagan 2006; Dagit et al. 2007; Dagit et al. 2009; Stillwater Sciences et al. 2010) to create a conceptual model to describe the factors that resulted in extirpation, supported re-colonization, the habitat interactions affecting their current population dynamics, and management implication for protecting the sub-population from another extirpation event.

Conceptual Model

Life history

The relationships between fish exhibiting resident and anadromous life history strategies in the Topanga Creek watershed are central features of an *O. mykiss* conceptual model that could apply to many southern California coastal streams. The primary factors influencing the expression of an anadromous life history in Topanga Creek are the frequency and duration of upstream migration opportunities, which are limited by lagoon sandbar formation and other obstacles, such as a seasonally dry reach from rkm 0.5 to 1.5 and additional low-flow barriers. Adult steelhead can only enter Topanga Creek on one of the relatively rare days each year that stream flows are high enough to erode the sand bar and allow passage between the ocean and lagoon. Under current conditions resident *O. mykiss* continue to spawn and maintain a sub-population despite the absence of production from anadromous individuals. However, it is the anadromous component of the metapopulation with adults that migrate among sub-populations, and the production of anadromous smolts, which allows salmonids to persist in an environment that experiences catastrophic disturbance (Reeves et al. 1995). After *O. mykiss* were extirpated from Topanga Creek in the 1980's it was the eventual migration of adult anadromous steelhead that provided for re-colonization. The current population is now occasionally influenced by the migration of anadromous adults either from Topanga Creek, or other sub-populations (Table 1).

Colonization

Until 1980, a sub-population of *O. mykiss* was known to be present in Topanga Creek (Moyle et al. 1989; Swift et al. 1993; Dagit et al. 2005). During a February 1980 storm event 65 cm of precipitation was recorded within a week, with a peak on 16 February of 27 cm within 24 hours. The accompanying flood was estimated to be an 83-year event,

Table 1. Observations of *O. mykiss* and number of days each year that steelhead passage into Topanga Creek may be possible, 2001–2010. Anadromous adults defined as greater than 450 mm FL with silver color.

Year	Mean number observed per month (all size classes)	Numbers observed per month (range)	Smolts	Anadromous adults	Redds	Annual total rainfall (cm)	Potential passage opportunity (days)
2001	53	2–122	0	1	0	70.6	10
2002	95	8–156	0	2	0	18.4	1–2
2003	59	6–72	14	1	0	45.5	10–15
2004	103	46–209	0	0	0	33.4	<10
2005	71	49–80	0	0	0	156.4	>200
2006	75	48–409	9	1	3	53.8	<20
2007	86	30–166	0	2	0	71.2	approx. 54
2008	316	40–691	1	1	0	33.5	approx. 72
2009	207	117–323	1	0	0	42.6	approx. 50
2010	253	117–420	28	1	4	61.7	approx. 50[b]

with flows recorded over 13,000 cfs before the gage was destroyed. Massive damage resulted to the creek channel, banks, and roads along the mainstem of Topanga Creek (York 1992). Other potentially catastrophic floods took place in 1983 and 1994 (Dagit and Webb 2002). A few *O. mykiss* were reported in pools upstream of the lagoon in 1990 (Keegan 1990) but an electrofishing survey conducted by the California Department of Fish and Game in 1997 failed to observe *O. mykiss*, and it was assumed that the sub-population was extirpated (Dagit et al 2005). The extirpation of the Topanga Creek sub-population is consistent with the range contraction observed throughout the DPS, where Boughton et al. (2005) have documented that only between 58% and 65% of historic steelhead basins currently harbor *O. mykiss* populations.

During an exstensvie survey in July 1998, a single 10-cm *O. mykiss* was found in Topanga Creek. In 2000, three anadromous adult *O. mykiss* were observed, and it appeared that the habitat within Topanga Creek was in the process of being re-colonized (Dagit et al 2005). Numbers of *O. mykiss* in Topanga Creek have since increased, and monthly snorkel surveys conducted since June 2001 indicate that the sub-population is currently fairly consistent, averaging between 53–316 individuals observed per year (Table 1).

The results of a genetic analysis conducted on Topanga Creek *O. mykiss* indicate that the sub-population has very low genetic variability (Girman and Garza 2006, Stillwater Sciences et al. 2010) compared to *O. mykiss* from 60 coastal sub-populations in California (Garza et al. 2004), Topanga Creek fish exhibited about half the allelic diversity and 80% of heterozygosity. This is likely the result of founder effects; i.e., very small numbers of fish contributed to the ancestry of the Topanga Creek sub-population as a result of the recent colonization.

Subsequent to the re-colonization events the genetic composition shows a variable contribution of anadromous adults. For example, a decrease in the portion of the sub-population exhibiting hatchery ancestry between 2003 and 2006 is likely the result of a particularly wet winter and spring in 2005, when adult *O. mykiss* (of wild origins) had more opportunity to enter Topanga Creek. However, the number of tissue samples collected and analyzed between 2003 and 2008 was small, and random chance may have

skewed the results, or these results may reflect random variation due to the reproductive success of a few resident *O. mykiss* during this period. Straying of adult steelhead appears to be common in southern California streams (Clemento et al. 2009; Pearse et al. 2009; Garza et al., unpubl. data, National Marine Fisheries Service, Southwest Fisheries Science Center, Santa Cruz, California), which plays an important role in population spatial structure and genetic diversity, both which support population viability (McElhaney et al. 2000).

Factors affecting population dynamics of O. mykiss

A species' life history and the habitat available to it are among the many factors that can influence a population's ability to persist, grow, or decline. In addition, the factors affecting success vary between life-history strategies that are employed. For the anadromous portion of the population, migration opportunity, growth rate, size at ocean entry, ocean survival, and spawning success influence the dynamics of the Topanga Creek *O. mykiss* sub-population. For resident fish that produce offspring that may or may not emigrate to sea, freshwater habitat availability and predation are the main factors influencing the population. In any given year, habitat conditions may favor the relative success of one *O. mykiss* life-history type over another.

Distribution

Topanga Creek has no tributaries, and all life stages are confined to the main stem. Although in many watersheds a proportion of the *O. mykiss* will use tributaries for spawning and rearing, both Spina et al. (2005) and Boughton et al. (2009) report that, in other southern California coastal streams, summer rearing typically occurs in mainstem reaches, even if the fish spawn in tributaries. The implication for Topanga Canyon is that any disturbance to the watershed can potentially affect all life stages of the sub-population. For example, whereas the ability of salmonids to survive large floods has been documented (e.g., Bell et al. 2001), during the catastrophic 1980 and 1983 floods every individual of the *O. mykiss* sub-population would have been in the mainstem (with the exception of sub-adults or adults in the marine environment), and thus susceptible to the impacts of the floods. If Topanga Creek had tributaries that supported rearing habitat, increasing spatial distribution of individuals throughout the watershed, it would take a much more severe disturbance to eliminate the sub-population (Reeves et al. 1995).

A key component of a functioning viable salmonid metapopulation is population spatial structure (McElhaney et al. 2000). Within a functioning and viable metapopulation, when a disturbance eliminates the individuals within one sub-population, anadromous individuals from the other watersheds eventually migrate to, and re-colonize, that habitat. We believe the catastrophic disturbances such as what occurred in the 1980's in Topanga Creek are a natural occurrence (Reeves et al. 1995), and it is the spatial structure (i.e., connectedness through migration) of various watersheds in southern California that allowed the sub-population in Topanga Creek to recover, and for the DPS metapopulation to be viable over time (McElhaney et al. 2000).

Spawning

The assumption used in our general conceptual model for steelhead (and other anadromous salmonid populations) is that population growth tends to be limited by rearing habitat because the number of eggs that can be deposited in a reach (and thus the number of fry produced by spawners) is usually very high relative to the amount of

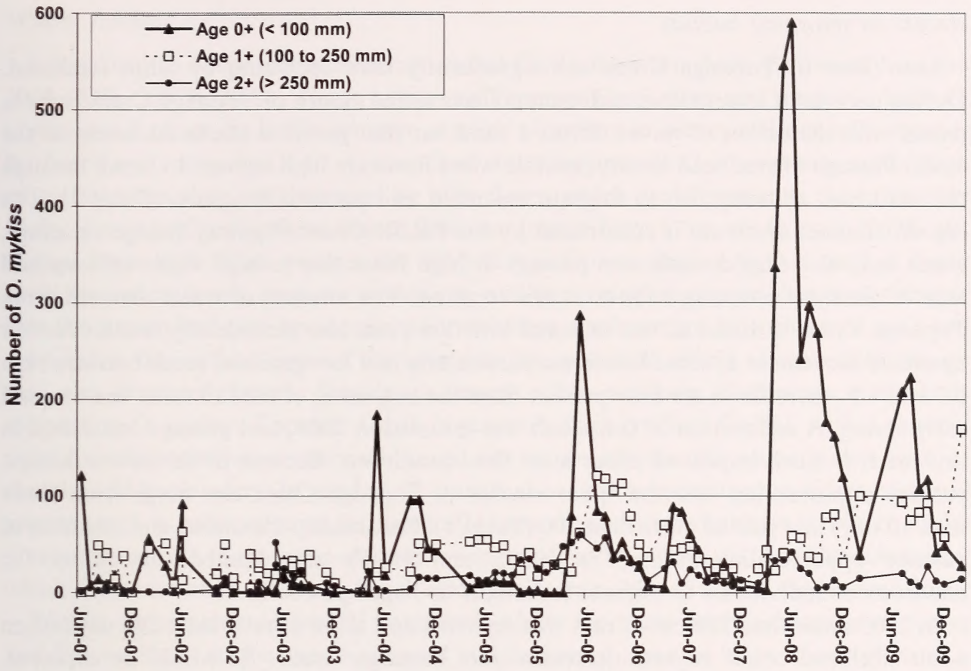

Fig. 1. Total number of *O. mykiss* observed in monthly snorkel surveys in Topanga Creek, June 2001–February 2009, by age class. Aging based on Stillwater Sciences et al 2010.

rearing habitat available as fish grow. However, in Topanga Creek, fry production does not appear sufficient to seed available rearing habitat. Because adult steelhead fecundity (usually >3,000 eggs per female) is much greater than that of resident female *O. mykiss* (usually <1,000 eggs [Moyle 2002]), population dynamics are potentially very different in years when anadromous individuals spawn versus years in which only resident *O. mykiss* spawn. Steelhead do not spawn every year in Topanga Creek. Fry production in years when adult steelhead can enter and spawn in Topanga Creek may be far greater than in years when only resident fish spawn. This phenomenon may be one reason that production of age 0 appears to fluctuate dramatically between years (Figure 1) as compared with populations in streams where anadromous individuals spawn every year.

Spawning habitat in Topanga Creek appears more than sufficient to support the relatively low numbers of resident and anadromous adults in the sub-population. Spawning gravels in Topanga Creek appear well-sorted, with embeddedness measurements generally ranging between 25 and 50%. Snorkel surveys have documented fewer than 600 age 0 in all years (Figure 1), indicating that egg-to-emergence or fry survival may be low. Observations of relatively low ratios of age 0 to age 1 juveniles (Stillwater Sciences et al. 2010) suggest that reproductive success is limiting production—even if only one or two *O. mykiss* redds were successful, age 0 fish should outnumber age 1 fish to a much greater degree than observed. Based on current spawning habitat quantity and quality, we believe that the low abundance of age 0 fish is more likely due to the fact that anadromous adults only infrequently spawn in Topanga Creek. Two other possibilities for low numbers of age 0 fish are (1) snorkel surveys are not very effective for observing this age class, and (2) age 0 fish experience high mortality rates due to occasional high spring flows (Fausch et al. 2001) or predation, as discussed below.

Access to spawning habitat

Low flows in Topanga Creek can significantly limit spawning by adult steelhead. During periods of lower flows, sediment collects at the mouth of Topanga Creek, which, paired with the action of waves, forms a sand bar that prevents steelhead access to the creek. Passage of steelhead is only possible when flows are high enough to break through the sand bar, allowing fish to migrate upstream and potentially spawn (Table 1). The lagoon channel upstream is constricted by the Pacific Coast Highway Bridge structure, which may also impede upstream passage at high flows due to high water velocity and lack of slackwater resting habitat at this location. The amount of water diverted from Topanga Creek is minimal, but seasonal low flows can also periodically restrict further upstream movement at some locations, particularly in a low-gradient reach between rkm 0.5 and 1.5 where flows are only present from the beginning of the fall rainy season until early spring. A restoration of this reach was initiated in 2008, and passage restriction in this reach is much improved under most flow conditions. Because of the above factors, passage opportunities into the upper reaches of Topanga Creek can range from fewer than 10 days in a year to more than 200 (Table 1). Presumably the timing and duration of passage opportunities during the 1980's and 1990's also limited the ability for anadromous individuals to migrate to habitat in Topanga Creek.

In 2005 more than 150 cm of rain was reported and there were at least 200 days when adult steelhead could migrate upstream into Topanga Creek. As would be expected, young-of-the-year fish were extremely abundant the following spring. Similarly, in 2007 there was relatively high rainfall and ample opportunity for passage, and the abundance of young-of-the year reported in 2008 was the highest recorded. By way of contrast, prior to 2004 upstream passage was possible fewer than 10 days each year, and the lowest numbers of age 0 were reported (Figure 1). Production in these years was presumably almost entirely (and perhaps exclusively) the product of spawning by resident fish.

Summer habitat

Summer rearing habitat has been posited to limit *O. mykiss* smolt production in some California coastal streams where a lack of habitat complexity, low pool volumes, low food availability, and excessive water temperatures may all act to reduce rearing success (e.g., Harvey et al. 2006; Stillwater Sciences 2007a). Topanga Creek appears to contain high-quality summer rearing habitat, with high pool frequency, abundant food, and ample cover supplied by interstitial spaces between cobbles and boulders in the substrate. Because food and space requirements increase as fish grow, a reach of stream will typically support far fewer age 1 than age 0 *O. mykiss* during the summer. In Topanga Creek, older age classes tend to be found in deep pools with abundant cover provided by wood or large substrate, and younger age classes in shallower step-pools and riffles (Stillwater Sciences et al. 2010). If *O. mykiss* abundance was limited by summer rearing habitat, we would expect to see higher numbers of all age classes in spring than in fall, but fall snorkel counts of age 0 fish are typically similar, if not higher, than spring counts (Figure 1), although this may be partly due to the difficulty of observing younger age classes using snorkel survey methods. In Topanga Creek it appears that shallow, structurally complex habitat is more than adequate to support numbers of age 0 fish in the summer, and sufficient deeper pool habitat is also available for over summering age 1 juveniles.

Winter habitat

In contrast to observations in many central California watersheds (Stillwater Sciences 2004, 2006, 2007b, 2009), winter habitat in Topanga Creek does not appear to limit *O. mykiss* production. As in the summer, a reach of stream in winter will typically support far fewer age 1 than age 0 *O. mykiss*. Overwintering juvenile *O. mykiss* may suffer high mortality when they are displaced by high flows, which are common in the inherently flashy Topanga Creek, where winter flows can range from a few cfs to over 10,000 cfs. Refuge from high flows requires the availability of cover similar to that used at lower flows for concealment, predator avoidance, and territorial boundaries, but access deeper into the stream bed may be necessary for avoiding displacement by turbulence near and even below the surface layer of the substrate (the potential effects of embeddedness on this are discussed later). Similar to many other southern California watersheds supporting *O. mykiss*, Topanga Creek is generally high gradient (>3%), with a channel tightly confined between valley walls and few or no off-channel water bodies such as sloughs and backwaters. In general, *O. mykiss* show less propensity than other salmonid species (such as coho salmon) for using off-channel, slackwater habitats in winter, and a greater propensity for using in-channel cover provided by cobble and boulder substrates, which are common in Topanga Creek and usually immobile at all but the highest flows.

Within our conceptual model, watersheds where there are increased inputs of coarse and fine sediment to the stream channel and decreased input of large wood (often as a result of anthropogenic disturbance), there is a reduction in summer and winter carrying capacity for age 0 and age 1 *O. mykiss*. Pool frequency is reduced with the removal of large woody debris, especially in forced pool-riffle and plane-bed stream reaches (Montgomery and Buffington 1997, Harrison and Keller 2007). High gradient, confined creek channels supporting little large woody debris, such as that found in Topanga Creek are typically characterized by forced pool-riffle sequences (step pools) resulting from boulder cascade constraints. The remaining pools may become shallower as a result of aggradation and the lack of scour-forcing features such as large woody debris, and cover may also be reduced. The filling of interstitial spaces within cobble/boulder substrates by gravel and sand can also reduce summer and winter carrying capacity for both age 0 and age 1 *O. mykiss*. As a result, in many watersheds the availability of winter rearing habitat limits *O. mykiss* production. However, sediment supply to Topanga Creek is currently limited to low levels of road shoulder dry-ravel, localized eroding slope input, and infrequent natural events, and the transport capacity of the channel appears adequate to move that sediment through the system. As a result, embeddedness is generally low and interstitial spaces within cobble/boulder substrates are abundant.

Data from snorkel surveys prior to and following high winter flows indicate that abundance of juveniles and adults generally does not decline as a response to high flows (Figure 2). Under current conditions it does not appear that winter habitat is limiting the Topanga Creek *O. mykiss* sub-population from persisting. However, clearly the extreme flood events of the 1980's were of sufficient magnitude to lead the extirpation of nearly all individuals from the watershed.

Water temperature and growth

Despite relatively high summer and fall water temperatures, *O. mykiss* in Topanga Creek appear to grow quickly, rapidly attaining a size favorable for smolt survival or for resident fish to reach sexual maturity. Growth only occurs when energy input is greater

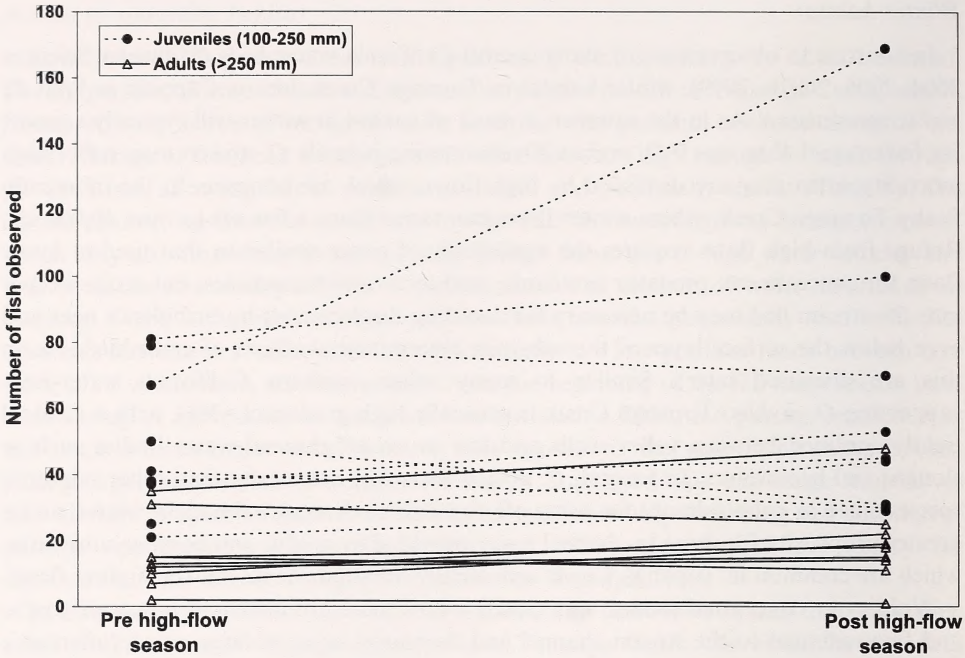

Fig. 2. Snorkel observations from pre- and post-high-flows for juvenile (100–250 mm) and adult (>250 mm) *O. mykiss*. Each line represents a separate year of observation from 2001–2009. Month of observation varies based on occurrence of peak flow event.

than energy expenditure, both of which can be affected by food availability and other environmental factors, especially water temperature (Jobling 1994).

Numerous studies have examined the relationships between water temperature and growth in *O. mykiss*. Results regarding optimal water temperatures for growth, and temperatures that may be detrimental due to increased metabolic demands, vary between study populations. Water temperatures in Topanga Creek are generally within the optimal range for *O. mykiss* growth in the spring and fall (Figure 3); however, daily maximum water temperatures over much of the summer regularly exceed species preferences and reported tolerances (>24°C) in all years monitored. It has been shown that lethal temperatures for *O. mykiss* are higher when fish have previously acclimated to high (but sublethal) temperatures (Cherry et al. 1977; Threader and Houston 1983). Further, Spina (2007) hypothesized that *O. mykiss* in Topanga Creek and other southern California streams tolerate higher water temperatures and have a higher temperature range for optimal growth than more northern populations.

O. mykiss in the southern part of their range appear able to sustain high growth rates when water temperatures are at the upper end of those considered optimal for growth, as long as food availability is high (Boughton et al. 2007). In Topanga Creek, *O. mykiss* appear to grow year-round, with potentially higher growth rates possible in spring and summer, and lower growth rates in winter (Stillwater Sciences et al. 2010). The size-at-age distribution of fish observed in Topanga Creek is consistent with the size of *O. mykiss* in comparable streams (Table 2), indicating that food availability is sufficient to counteract negative effects of increased temperatures on growth.

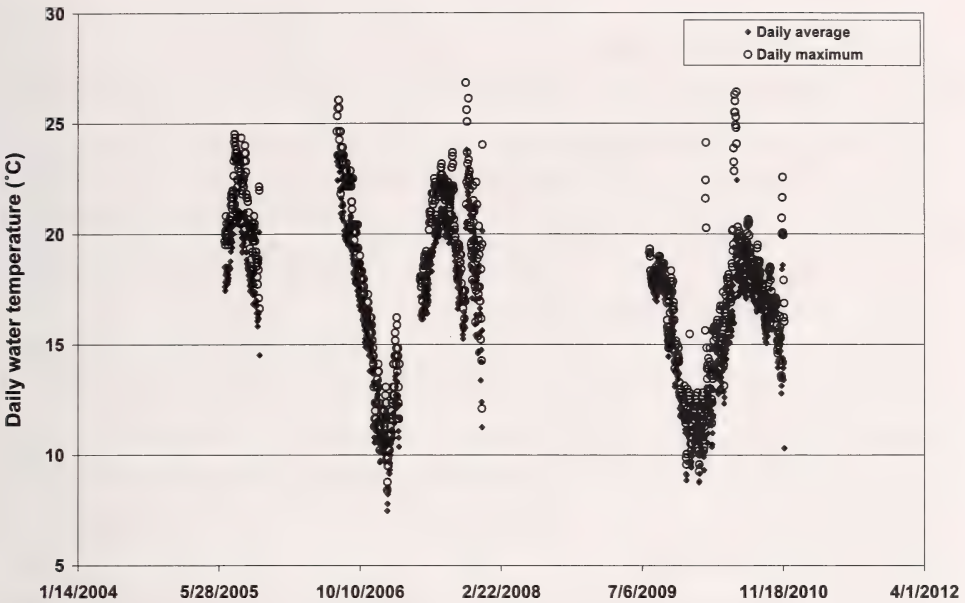

Fig. 3. Average (mean) and maximum daily water temperatures in Topanga Creek, 2005–2010.

Food availability

The ability of *O. mykiss* in Topanga Creek to grow quickly and reach large size (>250 mm) raises questions about how these fish meet their bioenergetic demands. Once salmonids reach a size of about 270–300 mm, they tend to become piscivorous regardless of habitat type, and a piscivorous or even cannibalistic diet may be necessary to maintain growth beyond this size (Bannon and Ringler 1986; Huryn 1996; Keeley and Grant 2001). Although piscivory in lake-dwelling trout populations is common, stream-dwelling resident *O. mykiss* most often feed on invertebrates and evidence of piscivory or cannibalism is rarely observed (Frost 1939; Jonsson and Sandlund 1979; Haraldstad et al. 1987, all as cited in Vik et al. 2001). Certain conditions, however, may facilitate the adoption of a piscivorous diet. For example, rainbow trout are known to prey on sockeye and chum salmon fry or smolts where such prey are concentrated, such as in small coastal streams or the outlets of lakes (McCart 1967; Hartman et al. 1967; Ginetz and Larkin 1976; Ruggerone and Rogers 1984; Fresh and Schroder 1987).

Table 2. Size of *O. mykiss* in Topanga Creek and other coastal southern California streams.

Stream	Sampling period	Fork Length (mm)		Age class
		Mean	Range	
Topanga Creek (this study)	November 2008–2009	102 (n=89)	55–125	0
		153 (n=79)	110–226	1
		222 (n=19)	170–291	2
Ventura River (Capelli 1997)	April 1995	250 (n=47)	190–395	unknown
Santa Paula Creek	November 2007 (electrofishing)	98 (n=173)	68–214	all ages

With only minor exceptions, forage fish available to adult resident *O. mykiss* in Topanga Creek are either smaller *O. mykiss* or arroyo chub (*Gila orcutti*). As mentioned above, very low numbers of age 0 trout have been observed in Topanga Creek during most years when snorkel surveys have been conducted (Figure 1). Even if only one or two redds were successful, observations of age 0 trout would be expected to be much higher than has been observed in all years, especially in years when spawning of anadromous *O. mykiss* occurs. It may be that snorkel surveys are inadequate for observing age 0 *O. mykiss*; however, their low abundance may also reflect heavy predation by resident adult *O. mykiss*. If this hypothesis is correct, the abundance of the *O. mykiss* sub-population in Topanga Creek may be limited by such predation.

Vik et al. (2001) found that cannibalism controlled brown trout mortality in a regulated stream and cites Amundsen (1994) as showing that even low rates of cannibalism (in this case, by Arctic char) may have substantial effects on recruitment. In Vik et al.'s (2001) study, cannibalism appeared to be facilitated in streams with adequate pool habitat for large individuals, but where refuge habitat for small trout was limited. Streams having coarse substrate and relatively low discharge, such as Topanga Creek, tend to exhibit these characteristics (Heggenes 1988, as cited in Vik et al. 2001). If such cannibalism is occurring in Topanga Creek, we would expect resident *O. mykiss* abundance to be limited by adult habitat (as described below) only in years when numbers of adults exceed the carrying capacity of available habitat. In addition, based on apparently very high winter and summer habitat availability in Topanga Creek, we might expect that the portion of the adult population expressing an anadromous life history could be limited by cannibalism of fry by adult resident fish, particularly if adult resident trout exhibit a functional response to the concentration of prey afforded by seasonal spawning and emergence of large numbers of *O. mykiss* fry.

Observations of arroyo chub in Topanga Creek show them to be consistently abundant, likely a result of their ability to breed almost continuously from February through August (Moyle 2002). Arroyo chub range in size from 3 to 150 mm, with approximately 10 to 50 individuals observed in nearly every pool. The high standing crop of arroyo chub suggests that either (1) predation pressure on chub is low, or (2) predation rates are high but the chub population remains high due to high rates of production. Although trout predation on arroyo chub has not been previously documented, examination of stomach contents in November 2010 revealed a mostly whole approximately 70 mm chub in the stomach of a 173 mm *O. mykiss* indicating that they may represent a potential food source for *O. mykiss* in Topanga Creek (R. Dagit, unpublished data).

Another potential food source for adult trout in Topanga Creek is the non-native red swamp crayfish (*Procambarus clarkii*). Although they had only a limited presence in Topanga Creek as recently as 2004, they are now widespread throughout the creek. Crayfish have been documented to reduce the complexity of food webs in stream ecosystems by consuming and consolidating energy from a wide variety of prey (Momot 1995). However, for the same reason, crayfish also represent high-calorie prey commonly consumed by trout (Momot 1967), and were found in three resident *O. mykiss* stomachs that were sampled in 2009 (Stillwater Sciences et al. 2010) and were also observed in two adults sampled in 2010 (R. Dagit, unpublished data). The presence of this additional high-calorie food supply in Topanga Creek could reduce cannibalism. Investigation of the diet of *O. mykiss* in Topanga Creek using gastric lavage began in November 2010 to further assess food availability and bioenergetics.

Smolt size and marine survival

The rate of growth of *O. mykiss* in fresh water has a direct effect on whether fish follow an anadromous or resident life history, as well as the ability to reach a size where they are large enough to smolt and survive in the marine environment (Satterthwaite et al. 2009). In addition, the ability of a sub-population to produce anadromous smolts is a key aspect of population spatial structure that can help increase population viability (McElhaney et al. 2000). For example, anadromous smolts may migrate to other watersheds within the metapopulation thereby increasing genetic exchange, or rear in the ocean prior to returning to spawn, thus avoiding potential disturbance events in the freshwater environment. *O. mykiss* juvenile growth rates in Topanga Creek appear sufficient to promote high ocean survival of smolts emigrating from Topanga Creek. The size of *O. mykiss* smolts has been positively correlated with marine survival, with smolts greater than 170 mm typically experiencing high survival (>10%) (Ward et al. 1989). Similarly, Bond et al. (2008) found that most adult steelhead returning to Scott Creek (central California coast) had entered the ocean as juveniles with an average fork length of just over 180 mm.

The size of smolts observed in Topanga Creek appears consistent with those observed in other southern California streams (Table 2). For example, in the Santa Clara River, most smolts measured at the Freeman Diversion Dam in 2009 were larger than 150 mm FL, averaging 185 mm FL (Steve Howard, Fisheries Biologist, United Water Conservation District, pers. comm., 2010). Kelley (2008) observed that most smolts in the Santa Clara and Santa Ynez estuaries were greater than 170 mm FL. Juvenile *O. mykiss* observed in the Ventura River during spring 1995 were all greater than 190 mm FL, and nearly all were age 2 when captured (n= 52) (Capelli 1997). Most of these fish were more than 3.2 km from the ocean, and it is not known what proportion were smolt, juvenile, or resident *O. mykiss*. Although other watersheds along the central coast of California report high growth rates of *O. mykiss* in lagoons prior to ocean entry (Smith 1990; Bond et al. 2008), poor habitat conditions in the Topanga lagoon may not be conducive to fish using this life-history strategy. Although juvenile steelhead may also remain and grow in the lagoon before entering the sea—we have rarely observed any *O. mykiss* in Topanga Lagoon. In early March 2010, we observed 28 juvenile *O. mykiss* in the Topanga lagoon but they disappeared within 24 hours following a high tide and good passage opportunity to the ocean (R. Dagit, unpublished data).

Data on the size of smolts emigrating from Topanga Creek is available from trapping conducted on an opportunistic basis, which suggests that many of the smolts are emigrating at fork lengths greater than 170 mm (Bell et al. *in press*). In addition, the trap is located at rkm 1.3, and our monitoring of PIT-tagged fish (in which there were multiple detections over several days), suggest that they migrate downstream very slowly, meaning that fish measured as smaller than 170 mm when captured in the trap may grow even larger before entering the ocean (Stillwater Sciences et al. 2010). For example, during the February 2010 snorkel survey, six smolts were observed in Topanga Creek downstream of the trap nearly a month after being observed at the trap. In other survey years, nearly all fish observed at the traps after February were larger than 170 mm, suggesting that smolts continue to grow during spring and likely enter the ocean at larger sizes than we observed at the trap in January.

Adult habitat limitations

As discussed above, resident *O. mykiss* occur in Topanga Creek. Resident *O. mykiss* are well adapted to surviving in small watersheds with high temperatures and variable flows by being highly territorial (Moyle 2002), growing at relatively fast rates (e.g., Hayes et al. 2008), reaching maturity as young as age 1 and as small as 130 mm (Moyle 2002), and by spawning multiple times. Adult habitat for resident salmonids is typically saturated if recruitment rates, even if very low, are sufficient to maintain the population (Elliot and Hurley 1998; Morita and Yokota 2002). Therefore, in most trout populations we usually assume that the resident population is limited by adult habitat; however, it is not clear that adult habitat is limiting the resident trout abundance in Topanga Creek. The most effective test to determine whether adult habitat is limiting is to increase the amount of habitat preferred by adults and observe any subsequent population response, which is often challenging, if not impossible. High flows in Topanga Creek in 2005 effectively eliminated low-flow migration barriers and adult trout were observed as far upstream as rkm 5.3 for the first time since 2000, increasing potential *O. mykiss* habitat by 900 m. The adult (age 2) population appeared to increase in that and subsequent years (Figure 1), suggesting that adult habitat had been limiting before. The apparent dramatic variability in numbers of adult trout in Topanga Creek may indicate that (1) habitat at an earlier life stage is limiting, as discussed above, (2) habitat availability changes as flows fluctuate among seasons and years, or (3) it could simply be an artifact of the challenges involved in observing *O. mykiss* during daytime snorkel surveys.

Summary

Based on nine years of data we have developed a general conceptual model for *O. mykiss* in Topanga Creek. Based on a relatively small abundance of smolts observed, the Topanga Creek sub-population is most likely an example of a "satellite" population (McElhaney et al. 2000). As a satellite population, it receives production from other sub-populations, but contributes little production to the metapopulation. Although satellite populations are more prone to extinction (as demonstrated by the temporary extirpation in the 1980's), they also buffer the metapopulation from disturbance events, can serve to increase metapopulation viability, and may become a source population in the future.

In general, the sub-population seems to be persisting since being re-colonized in the late 1990's, despite high summer water temperatures and poor habitat conditions in the lagoon. Migration from anadromous individuals in the metapopulation provided for re-colonization, and continues to influence the dynamic of the sub-population. Key factors believed responsible for supporting persistence of the sub-population are that fish can employ both resident and anadromous life histories, high-quality summer and winter rearing habitat, and food availability sufficient to maintain growth at high water temperatures. Additional data could be used to test and refine this model, focusing in particular on diet and use of the lagoon. We believe that the relatively high-quality rearing habitat in Topanga Creek should continue to be protected, especially from changes to the flow regime and increased sediment input, to guard against future extirpation. This is especially important since *O. mykiss* in Topanga Creek are exclusively distributed within the mainstem. The Topanga Creek Watershed and Lagoon Restoration Feasibility Study (Dagit and Webb 2002) outlined a series of potential actions to improve the condition of the lagoon, and prioritized the removal of the instream barrier presented by the Rodeo Grounds Berm, and streambank stabilization and channel restoration in the Narrows reach located at rkm 2–2.2. The passage

problems presented by the combined constraints of the lagoon and berm were also identified as the keystone barrier for steelhead in Topanga Creek (CalTrout 2006). The Rodeo Grounds berm was removed in 2008 and passage, spawning and rearing habitat in this 1.3 km reach are much improved. The restoration of the lagoon is being considered within the revision of the Topanga Creek State Park General Plan, and the Narrows project is awaiting additional Caltrans funding. Implementation of this trio of projects would improve passage and habitat conditions throughout the entire anadromous reach to support population spatial structure.

In addition, other watersheds within the DPS that do not currently support *O. mykiss* should be recognized for their potential contribution to the metapopulation. As was demonstrated in Topanga Creek, if habitat within watersheds such as Solstice, Arroyo Sequit, Trancas, Zuma, and Ballona creeks is restored they could once again support subpopulations and increase the viability of the metapopulation.

Acknowledgements

This work was funded by a grant from California Department of Fish and Game (Contract No. P0750021). We would like to extend special thanks to Mary Larson, Chris Lima, John O'Brien, Chris McKibbin, and Ken Robledo of the California Department of Fish and Game. Suzanne Goode, Nat Cox, and Kristy Birney were among the many California State Parks employees who supported our efforts. Stan Glowacki of NMFS, Sandra Albers and Mary Larson generously analyzed over two hundred scales. Steve Williams, Sandra Albers, Jayni Shuman, Delmar Lathers, Jenna Krug, Trevor Lucas, and Mark Wade provided essential field support. Anthony Clemento, Kerstin Avitabile, and Hilary Starks of the Genetic Analysis Team at NOAA's Santa Cruz Lab, and the employees and students of the Molecular Ecology Department at the University of California, Santa Cruz contributed to the genetic data collection and analysis. Much of the information used in this report is a result of the efforts of the volunteer members of the Topanga Creek Stream Team including core volunteers: Conor Driscoll, Nathan Moffatt, Karine Tchakerian, Ken Wheeland, and Ken Widen. This article benefited greatly from the careful review and suggestions from Angela Percival, Dr. Bruce Orr, Dr. Marc Capelli, Dr. Sabrina Drill, and Dr. Camm Swift. The comments of three anonymous reviewers were gratefully incorporated.

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Bull. Southern California Acad. Sci.
110(1), 2011, pp. 17–24
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Effects of Burial Depth and Substrate on the Emergence of *Bromus rubens* and *Brassica tournefortii*

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Abstract.—The germination of seed is critical in deserts where annual plants are abundant and rely on seed buried in the soil for sustaining populations. The exotic annuals *Bromus rubens* and *Brassica tournefortii* threaten arid indigenous ecosystems such as the Mojave Desert, but little is known about the potential effects on seed emergence of different burial depths and substrates that could enhance or reduce emergence. Using seed from Mojave Desert populations, we conducted a three-factor greenhouse experiment testing the effects of species (*Bromus* or *Brassica*), burial depth (0, 2, 5, or 10 cm), and substrate (none, gravel, or litter) on seed emergence. Species and substrate interacted significantly with burial depth. Both species displayed the greatest emergence when seeds were sown on the soil surface (70% emergence for *Bromus* and 52% for *Brassica*), but *Bromus* emergence declined less at a 2-cm depth than *Brassica*. Emergence of surface-sown seed did not differ significantly among substrate types, but emergence of buried seed was significantly reduced below gravel substrates compared to no substrate or litter substrates. This suggests that seed fates in the soil (such as seed mortality by germination but not emergence from the soil) can be altered by manipulating soil surface conditions.

Introduction

Seed germination is the initiation of growth by the embryo within a seed, and emergence is the appearance of a seedling above the soil surface. These processes are critical in ecosystems and influence plant regeneration, habitat structure for biota, and seed resources available to granivores (Harper 1977). Seed ecology also plays key roles in contemporary biological conservation (Baskin and Baskin 2001). One of these roles is understanding the regeneration ecology of exotic species, to potentially aid in the development of management strategies to limit the establishment of exotics in indigenous ecosystems (van der Valk and Pederson 1989).

Two of the many factors that can affect seed emergence are the type of substrate on or below which seeds are located and the depth at which seeds are buried in the soil (Scoles-Sciulla and DeFalco 2009). Seeds can be dispersed onto a variety of substrates (e.g., leaf litter versus mineral soil), which can differ in the protection they afford to seeds and their penetrability by emerging seedlings. For example, Evans and Young (1970) found that placing seeds of the annual *Bromus tectorum* (cheatgrass) below 5 or 10 cm of herbaceous leaf litter increased fall and early spring emergence by 4- to 5-fold in a field experiment in the Great Basin Desert of western Nevada. Seeds can become buried at different depths in the soil through a variety of processes, such as water movement, interment by biota, or being covered by litter or dust (Harper 1977). Chauhan et al. (2006) illustrated the effects

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of burial depth on *Brassica tournefortii* (Sahara mustard; hereafter *Brassica*) using Australian seed lots in a greenhouse experiment. Emergence was 29% for seeds sown on the soil surface, 51% for seeds buried 1 cm deep, and zero at a depth of 5 cm. Knowledge of these types of factors can facilitate an understanding about controls on the establishment patterns of plants, including exotic plants (DeFalco et al. 2009). If seeds are buried to a depth (or within a substrate) where germination but not emergence occurs, or where seeds decompose, plant establishment could be reduced. Recently, for instance, Kollmann et al. (2011) proposed burying propagules as a potential treatment for reducing *Rosa rugosa* (Japanese rose), an exotic shrub in northwestern Europe.

Exotic, invasive plant species are considered a primary threat to indigenous ecosystems in the Mojave Desert (Steers and Allen 2010). Two of the most invasive species of concern are the annual grass *Bromus rubens* (red brome; hereafter *Bromus*) and the annual forb *Brassica*. The species provide fuel that facilitates the spread of fires destructive to late-successional shrub vegetation and compete with native plants (Lei 2006). The purpose of this study was to better understand factors potentially influencing the emergence of *Bromus* and *Brassica*, in particular 0–10 cm burial depths and simulated litter, gravel, and mineral soil substrates.

Methods

The Mojave Desert is in parts of California, Nevada, Utah, and Arizona, and is classified as a hot desert that receives the majority of its precipitation in winter (Smith et al. 1997). Shrublands dominated by *Larrea tridentata* (creosote bush) and *Coleogyne ramosissima* (blackbrush) typify the physiognomy of the desert at the lower and middle elevations (Lei and Walker 1997). *Bromus* and *Brassica* can be the dominant annual plants growing below shrub canopies, but both species also can become established in open areas especially during moist years (Beatley 1966, Trader et al. 2006). Human and non-human (e.g., animal burrowing) disturbances appear to promote the establishment of these exotics, but they can invade relatively undisturbed desert (Beatley 1966, Bangle et al. 2008).

Bromus is native to southern Europe, northern Africa, and southwestern Asia, occurring from sea level to 1,300 m in these regions (Brooks 2000). The species is thought to have been introduced to North America by the mid-1800s and was well established as a dominant annual in the Mojave Desert by the mid-1950s (Brooks 2000). *Brassica* is native to the semi-arid and arid deserts of North Africa and the Middle East and to the Mediterranean lands of southern Europe. This species is believed to have been introduced to North America in the early 1900s (Minnich and Sanders 2000). Seed weights reported for *Bromus* have ranged from 1.82–2.47 mg/seed (Royal Botanical Garden Kew, Wakehurst Place, England). Trader et al. (2006) reported a mean weight of 1.17 mg/seed for *Brassica* in the Mojave-Sonoran Deserts.

We collected seed of *Bromus* and *Brassica* in the eastern Mojave Desert of southern Nevada. We harvested *Bromus* seed in April 2008 from two sites approximately 400 m in elevation in Lake Mead National Recreation Area (LMNRA) and one site (Loop Fire) 1,100 m in elevation in Red Rock Canyon National Conservation Area. *Brassica* seed was collected from three sites in LMNRA ranging in elevation from 360–390 m. The LMNRA collection sites were near 36°00′N, 114°40′W and the Loop Fire site was near 36°00′N, 115°25′W. Seeds were stored at room temperature in paper bags in a laboratory until the experiment. A weather station (Boulder City, Nevada, 768 m in elevation) centrally located within LMNRA has reported averages of 14 cm/yr of precipitation, a

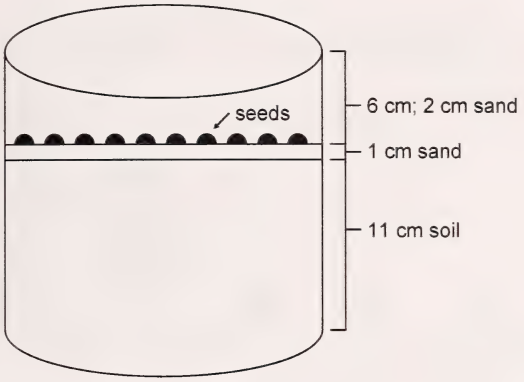

Fig. 1. Example of a treatment with a 2-cm seed burial depth, where 2 cm of sand are placed on top of the seeds. A substrate of litter or gravel would be added on top of the 2 cm of sand if required by a treatment combination.

July daily maximum temperature of 39°C, and a January daily minimum temperature of 4°C (1931–2004 records; Western Regional Climate Center 2010). The Spring Mountain Ranch State Park weather station, 7 km south of the Red Rock collection site and 1,152 m in elevation, has reported 29 cm/yr of precipitation, a July daily maximum temperature of 36°C, and a January daily minimum temperature of −1°C, averaged from 1977–2009 records (Western Regional Climate Center 2010).

The experiment was a randomized, full-factorial design consisting of three factors: two levels of species (*Bromus* and *Brassica*), four burial depths (0, 2, 5, and 10 cm), and three levels of substrate (none, litter, and gravel). Each of the 24 treatment combinations was replicated three times. We conducted the experiment in a greenhouse at the University of Nevada Las Vegas (Las Vegas, NV), with individual pots (3.8 L, 15 cm in diameter, and 18 cm tall) serving as replicates. Pots were filled with sterile potting soil (Kellogg Garden Products, Carson, CA) with 1 cm of sterile sand (all-purpose sand, supplied by Quikrete, Atlanta, GA) placed on top of the potting soil. The layer of sand was added so that seeds had contact with a sand layer resembling desert soils rather than the potting soil. Ten randomly selected seeds of the species assigned to a pot were evenly sown on top of the sand layer. Burial treatments entailed covering the seeds with additional sand so that seeds were buried to the appropriate experimental depths. The 0-cm level of the burial treatment had no sand added on top of the seeds and represented seeds simply sown on the surface. A substrate, if part of the treatment combination, was then placed on top of the seed (for the 0-cm burial treatment) or on top of the seed covered by the sand in the 2-, 5-, and 10-cm burial treatments (Fig. 1). For the substrate litter treatment, dead thatch material of approximately equal *Bromus* and *Brassica* was obtained from the seed-collection sites and shaken to remove unwanted material. Approximately 5 g of thatch were placed in a layer ca. 1 cm thick. We used a 1-cm thick layer of gravel (Quikrete all-purpose gravel, consisting of pebbles ca. 1 cm in diameter) for the gravel substrate.

We designed the treatments to mimic substrates to which seeds could be exposed in the field. Seeds in soil below shrubs must penetrate through litter to emerge, whereas seeds in openings must emerge on mineral soil, situations simulated by the litter and no substrate treatments. The gravel substrate treatment was selected to mimic coverage of seeds by mechanisms such as biopedturbation by small mammals (Whitford and Kay 1999) or

Table 1. Analysis of variance results for the influences of burial depth (0, 2, 5, or 10 cm) and substrate (none, litter, or gravel) on the emergence of seeds of *Bromus rubens* and *Brassica tournefortii* collected in the Mojave Desert.

Effect	Num DF[a]	Den DF[a]	*F*-statistic	*P*
Species	1	48	3.47	0.0687
Depth	3	48	44.69	<0.0001
Substrate	2	48	8.45	0.0007
Species × depth	3	48	3.69	0.0181
Species × substrate	2	48	0.39	0.6794
Depth × substrate	6	48	2.66	0.0262
Species × depth × substrate	6	48	0.75	0.6108

[a] Numerator and denominator degrees of freedom.

deposition in washes. Both species can inhabit washes in the Mojave Desert (Beatley 1966).

The experiment began in March 2009, when germination and emergence of the species occur in the field (Beatley 1966). We randomly arranged pots on a bench in a greenhouse maintained at a constant 24°C without supplemental lighting. Pots were hand watered to soil moisture capacity every two or three days and emergents were counted weekly for two months.

We analyzed the data as a fully crossed, three-factor experiment with the proportion of seeds emerging (out of 10 for each pot) as the response variable in an analysis of variance. We used PROC MIXED with Tukey adjustments for multiple comparisons in SAS software (SAS Institute 1999). Because some of the treatment combinations had no emergence and hence zero variance, we compared results of this model with *P* values computed through permutation using Cassell's (2002) macro for SAS. Permuted and normal approximation *P* values were identical to the hundredths place, so we report the *P* values from the normal approximation model.

Results

Species and substrate both interacted significantly with burial depth in influencing seed emergence (Table 1). Emergence of both species at a 0-cm (surface) depth was significantly greater than at 5- or 10-cm depths (Fig. 2). The species × depth interaction was related to the finding that *Bromus*' emergence at a 2-cm depth did not differ from its surface emergence, whereas *Brassica* had significantly lower emergence at 2 cm than at the surface. Similarly, emergence of surface-sown seeds did not differ among substrates, but seeds buried at a 2-cm depth exhibited sharp declines in emergence when gravel substrates were present. Only the litter treatment had appreciable seed emergence at 5- or 10-cm depths, albeit at levels significantly reduced compared to surface-sown seeds.

Discussion

Burial at depths > 2 cm and below gravel substrates sharply curtailed emergence of both *Bromus* and *Brassica*. However, *Bromus* displayed a stronger ability to emerge at a 2-cm depth than *Brassica*, resulting in a significant species × depth interaction (Fig. 2). Seeds of *Bromus* are 1.5- to 2-fold heavier than those of *Brassica* (Royal Botanical Garden Kew, Wakehurst Place, England; Trader et al. 2006). These seed weight-emergence patterns are consistent with the common observation that heavier seeds typically can emerge from greater depths than lighter seeds (Harper 1977).

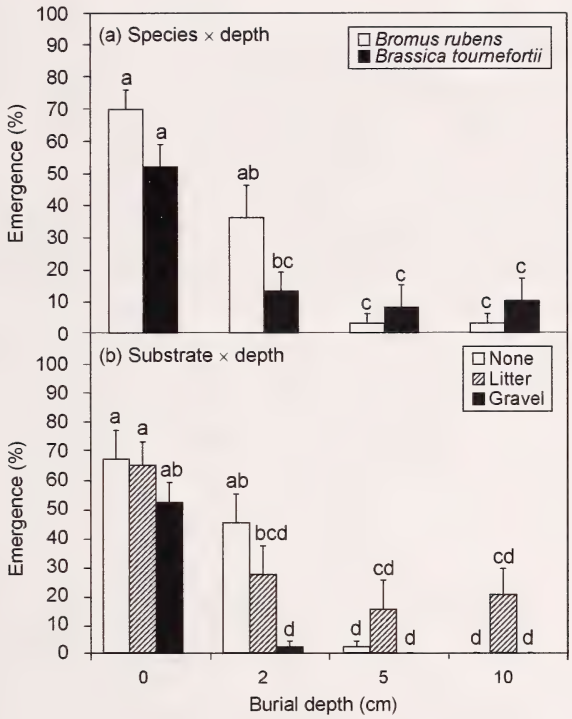

Fig. 2. Mean emergence of two annual plant species of the Mojave Desert in relation to burial depth and substrate treatments, for significant interactions shown in Table 1. Error bars are standard errors of the means. Means without shared letters, within (a) or (b), differ at $P < 0.05$.

While the literature is limited on burial and substrate effects on the emergence of these species, some previous studies of these and related species do permit comparisons with this experiment. Our results agree with a previous greenhouse experiment with Australian populations of *Brassica* where emergence was negligible when seeds were buried at depths of ≥ 3 cm (Chauhan et al. 2006). However, our results are incongruent with Chauhan et al.'s (2006) finding that more *Brassica* seeds emerged from 1–2 cm burial depths than on the surface, or the findings of Thanos et al. (1991) that more seeds of Greek populations of *Brassica* emerged when buried than at the soil surface. We found that emergence was greater for seeds sown on the surface than when buried at any depth. Thanos' et al. (1991) study was conducted outdoors, however, where exposure of seeds to weather and granivory (especially on the soil surface) could have reduced the seeds available to germinate, although it was not mentioned if seeds were open to predation by animals or invertebrates. These types of factors could have large effects on plant establishment in the field, where burial of the seeds below some soil could reduce granivory and protect seeds (DeFalco et al. 2009).

We found that litter had a minimal influence on *Bromus* or *Brassica* emergence, consistent with the observation that these species can become established below perennial plants in the Mojave Desert where litter accumulates (Strojan et al. 1979). What remains uncertain, however, is whether effects of different types of litter from different perennial species vary, or if depths of litter in the field could become sufficiently thick to hinder emergence. Working with *Bromus tectorum* in *Pinus ponderosa* (ponderosa pine) forests using a greenhouse experiment, Pierson and Mack (1990), similarly to our study, found

that emergence with and without 1.5 cm of *P. ponderosa* litter did not differ. However, a thicker litter layer, 6 cm, decreased emergence by 36%. In contrast, Evans and Young (1970) placed *B. tectorum* seeds below 5 or 10 cm of herbaceous litter in a field experiment in western Nevada's Great Basin Desert and found that emergence increased compared to without litter by 4- to 5-fold in fall and early spring. Litter could switch from positive (such as protecting seeds; DeFalco et al. 2009) to negative effects on seed emergence based on a variety of factors, such as the thickness or chemical composition of the litter. Further manipulating litter through field experiments that include different thicknesses of litter could be useful for assessing the potential role of litter in the establishment of exotic plants in the Mojave Desert.

Most of the burial depth research with annual *Bromus* species has concentrated on different questions than our focus on emergence. Several studies with *Bromus tectorum*, for example, have examined effects of burying packets or capsules filled with seeds on the viability and germinability of the seed when exhumed (e.g., Gleichsner and Appleby 1989, Burnside et al. 1996, Wicks 1997). These are central questions about the longevity of seed banks, but do not address depth effects on emergence *per se*. Findings from these studies suggest that *B. tectorum* seeds can germinate *in situ* (though not necessarily emerge) when deeply buried. Gleichsner and Appleby (1989), for instance, reported that 87% of seeds germinated within 30 days when buried at a depth of 30 cm in an agricultural field in western Oregon. These findings suggest that seeds in our experiment possibly germinated at the deep burial depths, but were not able to emerge, although this is not known with certainty for our study species.

The observed emergence patterns in the greenhouse of these species may reinforce some field patterns and highlight ideas that could benefit from further research. For instance, the finding that litter placed on top of seeds at the 0- and 2-cm burial depths did not influence emergence, relative to the no substrate treatment, supports the observation that seedlings of these species are abundant below perennial shrubs that have litter layers in the Mojave Desert (Strojan et al. 1979, Brooks 2009, Abella et al. 2011). It should be noted, however, that intrinsic effects of litter could interact with shade or other effects of the shrubs, vary with the type of litter, and differ in open- versus below-shrub environments. Nevertheless, both of our study species demonstrated the ability to emerge through a layer of their own litter at the 1-cm litter thickness we tested. In contrast, gravel as a substrate sharply decreased emergence at any burial depths $\geq$ 2 cm. This effect could partly relate to the added depth of dense material from the gravel that seeds needed to penetrate up through, as opposed to the low-density litter layer. Working with the native Mojave Desert perennial *Pleuraphis rigida* (big galleta grass) in a greenhouse experiment, Winkel et al. (1995) concluded that burial below 2–3 cm of gravel aided emergence, whereas thicker layers of 4–5 cm curtailed emergence. *Bromus* and *Brassica* occupy many different soil types in the Mojave Desert, but specifically testing soil particle size effects on emergence when seeds are sown on top of or below materials differing in particle size could help further isolate potential substrate influences. Results indicate that approximately 5 cm is the greatest burial depth from which reliable emergence can be expected for either exotic species.

Effects of the burial depths and gravel substrates support suggestions that a possible control treatment for the species is to bury seeds (or cover them with a substrate) to a depth where germination, but not emergence, occurs, or where viability is lost due to seed decomposition (Wicks 1997). This could deplete the seed bank over time. Gleichsner and Appleby (1989), for instance, suggested that tillage be used to bury seeds in western

Oregon agricultural fields for reducing *Bromus tectorum* emergence. Tillage is not necessarily practical in intact desert ecosystems due to non-target impacts on native vegetation and soils. However, the data do suggest a possibility that mulches (e.g., wood chips) or similar materials may form physical barriers to emergence.

Acknowledgments

This study was supported through cooperative agreements between the University of Nevada Las Vegas (UNLV) and the National Park Service (Lake Mead National Recreation Area, with Alice Newton and Kent Turner) and the Bureau of Land Management (Southern Nevada District, with Kevin Oliver, Nora Caplette, and Christina Lund). The research greenhouse at the UNLV provided space for the study, which was conducted as part of ENV 492 (Undergraduate Research) at the UNLV. Sharon Altman (UNLV) formatted the figures; Cheryl Vanier (UNLV) helped with the statistical analysis; and Sharon Altman and two anonymous reviewers provided helpful comments on the manuscript.

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Bull. Southern California Acad. Sci.
110(1), 2011, pp. 25–34
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Age and Growth of Two Herbivorous, Kelp Forest Fishes, the Opaleye (*Girella nigricans*) and Halfmoon (*Medialuna californiensis*)

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Abstract.—Opaleye (*Girella nigricans*) and halfmoon (*Medialuna californiensis*) are herbivorous sea chubs (Perciformes: Kyphosidae) that occupy an ecologically important role in kelp forests off southern and Baja California. This study provides information on length-weight relationships, age, and growth of these two ecologically important species. Opaleye and halfmoon were collected from throughout the Southern California Bight to evaluate these life history characteristics. Length-weight relationships were described by the equations $W = 0.00002L^{3.081}$ for opaleye and $W = 0.000003L^{3.454}$ for halfmoon. Sagittal otoliths were used to age opaleye from ages 3–10 and halfmoon from ages 0–8. In addition, age classes 0-II for opaleye were determined from length frequency analysis of preserved specimens. Von Bertalanffy growth curves were fitted to mean standard length (mm) at age for each species. Opaleye were aged up to 10 years whereas halfmoon was recorded up to eight years of age. Standard length-at-age growth curves were typical of nearshore marine fishes with rapid growth in the first few years, reaching an asymptote quickly thereafter. This study demonstrates opaleye and halfmoon are short-lived, fast growing species, and this information combined with other life history characteristics shows the importance of opaleye and halfmoon and the need for ecosystem-based management in kelp forest communities.

Introduction

Age and growth studies are essential for understanding the life history of fishes (Choat and Robertson 2002, King and McFarlane 2003, Pikitch et al. 2004, Depczynski et al. 2007). Furthermore, knowledge of life history patterns (e.g., age structure, diet, reproduction) is an important facet of fisheries science and should be a fundamental component of management strategies (King and McFarlane 2003). Traditionally, fisheries management has utilized life history information for a single species management approach. However, a major flaw of single species management is the lack of consideration of trophic interactions between target species and the non-target species on which the fishery ultimately depend (Pinnegar et al. 2000). In recent years, fisheries management has begun the slow shift towards utilizing ecosystem-based management (Pikitch et al. 2004). Unfortunately, progress has been hindered by several concerns and impediments that come along with this type of comprehensive management approach (Pinnegar et al. 2000, King and McFarlane 2003). One major obstacle to implementing ecosystem-based management is the lack of basic life history information available on

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non-targeted and/or newly exploited species (King and McFarlane 2003, Pikitch et al. 2004). As knowledge gaps of detailed life history information are filled, managers will be better equipped to implement more holistic fishery management strategies.

Opaleye (*Girella nigricans*) and halfmoon (*Medialuna californiensis*) are two of three herbivorous fishes found in the temperate waters of southern California and as adults, are closely associated with kelp forests (Quast 1968, Allen 1985). Of the three southern California herbivorous species, opaleye and halfmoon are the most abundant; therefore, these two species most likely have the ability to greatly influence the kelp forest community. Opaleye range from San Francisco, California to Baja California, Mexico, whereas halfmoon have a slightly more northern distribution ranging from Vancouver, British Columbia to Gulf of California, Mexico (Miller and Lea 1972). Although herbivorous fishes are rare in temperate waters, opaleye and halfmoon most likely play an essential role in maintaining and contributing to the complexities of the kelp forest food web similar to herbivorous fishes in other marine communities. Through constant grazing, opaleye and halfmoon may help maintain the algal balance in kelp forests by preventing an algal take-over, providing disturbance and potential for competition of other algal species and sessile invertebrates, and increasing nutrient input via excretions (Carpenter 1986, Hixon and Brostoff 1996). Additionally, opaleye and halfmoon contribute largely to the productivity of kelp forests communities. The combined annual production of opaleye and halfmoon within kelp forests at Santa Catalina Island is reported as 13.01 g WWt/m^2/yr (Bredvik 2008, Boerger unpub. data) have the potential to provide a significant amount of energy transfer (via predation) throughout temperate kelp forests and other adjacent nearshore communities. Both opaleye and halfmoon are essential to the functioning of kelp forest ecosystems and contribute indirectly and directly to the commercial and recreational fisheries. However, a thorough examination of opaleye and halfmoon life history patterns needed to be conducted before it would be possible to include either of these abundant fishes in the evaluation and management of nearshore fisheries in southern California. The purpose of this paper is to aid in filling the life history information gap by providing the 1) length-weight relationships, 2) age information, and 3) growth rates for these two ecologically important fishes.

Methods

Field Collection

Juvenile opaleye largely inhabit the rocky intertidal (in tide pools) and shallow subtidal areas and were, therefore, not represented in gill nets samples (see below) which provided freshly extracted and dried otoliths for age determination. Therefore, to determine age for young opaleye, we used preserved specimens taken from tidepools at Palos Verdes and Pin Rock, Catalina Island from 1982 to 1984. Larger opaleye were collected from June 2006 through October 2007 and all halfmoon were collected from February 2005 through May 2007 throughout the Southern California Bight (SCB) at several sampling stations (Figure 1). Fish were collected by a variety of means including spear on snorkel and SCUBA, hook and line, dip nets, and gillnets (Allen et al. 2007). Each fish was measured (head length, standard length, and total length) to the nearest millimeter and weighed with varying degrees of precision depending on the size of the fish. Smaller fish from approximately 20-mm SL to 60-mm SL were weighed in the lab with an analytical scale (± 0.0001g) and larger fish with a hand held spring scale aboard ship (± 1g).

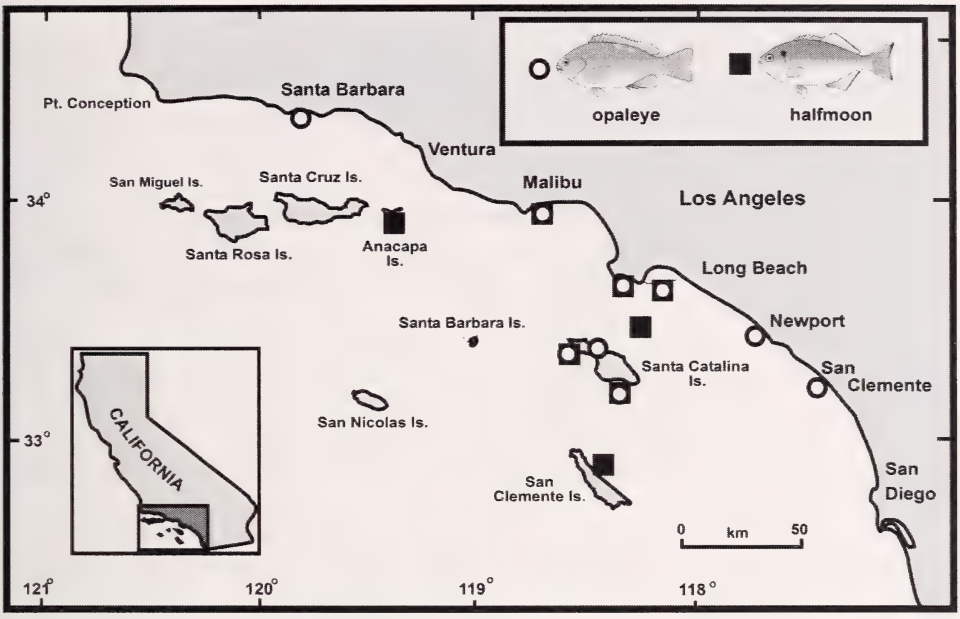

Fig. 1. Map of Southern California Bight indicating locations of field collection sites for opaleye and halfmoon.

Length-Weight Relationships

The length-weight relationships of opaleye and halfmoon were estimated by using the length-weight equation following the method of Ricker (1973) for fitting a nonlinear regression model by least squares. The equation is as follows:

$$W = aL^b$$

where W is total weight (g), L is standard length (mm), and a and b are constants, with values determined by the exponent function subroutine in *Excel* (MS Office 2007).

Otolith Preparation

Following collection of all measurements, sagittal otoliths were extracted, rinsed in distilled water, dried, and stored in small coin envelopes before sectioning. In most cases, the left otolith was used to obtain otolith morphometrics and age unless the left otolith was absent or in poor condition (i.e., broken), in which case the right otolith was used. The length and width of the sagitta was measured (± 0.01 mm) using digital calipers and weighed (± 0.0001 g) using an analytical balance. Each otolith was secured to an individual block of wood (approximately 20 × 10 × 5 mm) using cyanoacrylate glue. After allowing the glue to dry and set (~24 hours) otoliths were sectioned through the focus using a Buehler-Isomet low speed saw. The saw was equipped with two 0.3-mm diamond wafering blades and an acetate spacer which created a 0.75 mm thick transverse otolith section. Otolith sections were removed from the surrounding wood block and ground wet on both sides with 400 grit waterproof sandpaper until sections were approximately 0.5 mm thick, then polished using 600 grit lapping film. Transverse otolith sections were submerged in water in a small watch glass and examined under a dissecting microscope (20–40× magnification) with reflected light on a black background.

Age Determination and Growth Curves

To determine age for young opaleye, we used length frequency data from preserved specimens. Because preservation renders the otoliths of the specimens unusable for ageing, length frequency data from the preserved specimens were subjected to an age analysis as described in Pauly and David (1981). In this technique, length frequency is simply plotted in larger class intervals to smooth out small irregularities. A running average is then used to emphasize peaks and intervening troughs. Each frequency value is then divided by the corresponding running average frequency and plotted to identify the most likely center of the age classes represented. Individual fish are then assigned to the corresponding age classes based on size alone.

For older opaleye and all halfmoon, each complete pair of opaque and transparent bands (annuli) was counted as one year. All otoliths were read at least two times independently, an additional blind reading was made if the first two readings were not in agreement. If three readings were necessary the estimated age was determined as the matching values from two of the three readings. There were no cases of all three readings with different values.

Using age-class means to minimize the bias of highly abundant age classes, VONBIT version B software (ftp.fao.org/fi/stat/windows/vonbit/) was used to describe the standard length at age with the von Bertalanffy growth model equation:

$$L(t) = L_{\infty}\left(1 - e^{-K(t-t_0)}\right)$$

where L(t) is the standard length or weight at age t, L_{∞} is the asymptotic length or weight, K is the growth coefficient, and t_0 is the theoretical age at zero length.

Results

Length-Weight Relationships

The standard length and weight of opaleye and halfmoon collected ranged from 23–310 mm and 20–342 mm, and 0.17–1,147 g and 0.1–2,301 g, respectively. Standard length to total length conversions were TL = 1.221(SL) for opaleye and TL = 1.2366(SL) for halfmoon. The length-weight function for opaleye (n = 279) was calculated as $W = 0.00002L^{3.081}$ ($R^2 = 0.993$) (Figure 2). This relationship for halfmoon (n = 449) was $W = 0.000003L^{3.454}$ ($R^2 = 0.984$) (Figure 3).

Age and Growth

Age classes 0, I, and II were assigned to 216 juvenile opaleye from preserved samples by length frequency analysis (Table 1, Figure 4). Prominent peaks where found centered around the 60–75 mm, 150–180 mm, and 195–210 size intervals representing the Age-0, I, and II classes. Age assignments based on individual lengths yielded sample means of 58 mm SL for Age-0, 150 mm SL for Age-I, and 201 mm SL for Age-II opaleye (Table 1). Overall, 321 opaleye were used to determine age. Opaleye collected throughout the Southern California Bight ranged in age from age-0 (YOY) to a maximum of 10 years. Otolith weight was found to be a significant predictor of opaleye age ($R^2 = 0.69$, $P < 0.001$) and served as an indirect validation of the ageing technique (Choat and Axe 1996, Choat et al. 2009). Individuals used for ageing ranged in length from 24.5–302 mm standard length and in weight from 0.265–1,147 g.

A total of 269 otoliths were readable for the age analysis of halfmoon, yielding eight different size classes ranging from age-0 to eight (no fish were placed in the age-7 class).

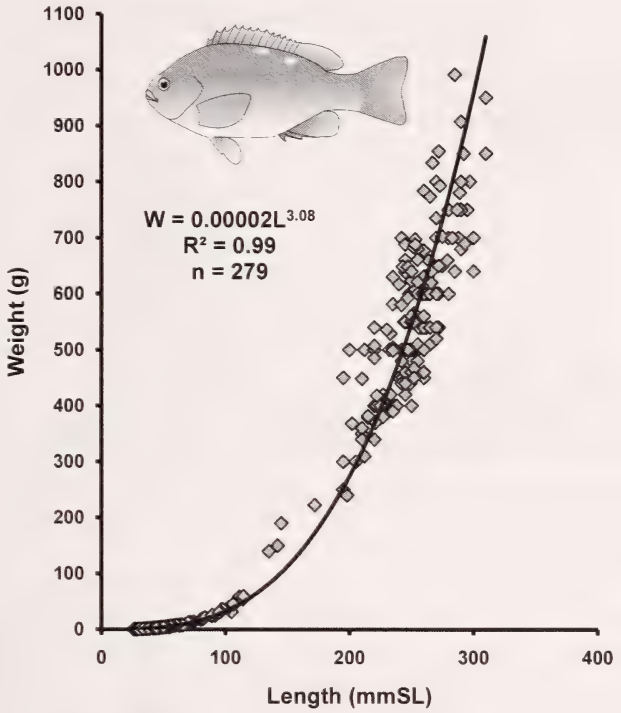

Fig. 2. Length-weight relationship of opaleye (*Girella nigricans*) based on 279 specimens.

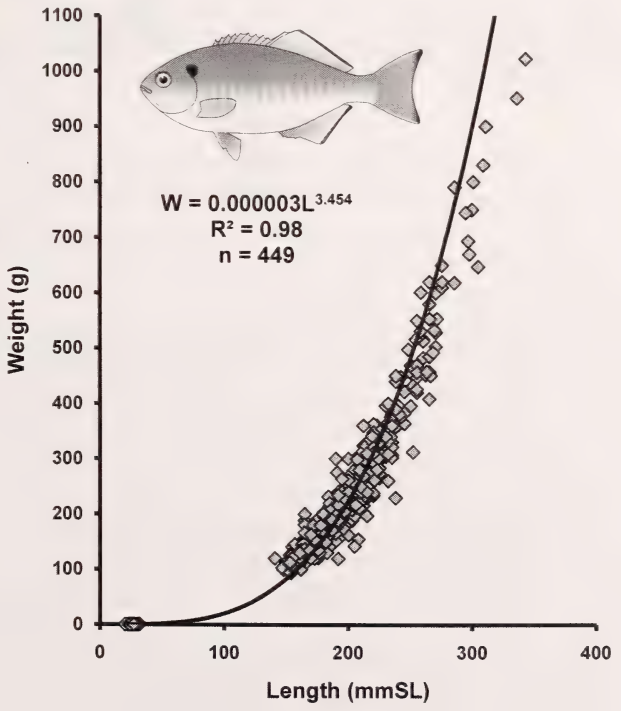

Fig. 3. Length-weight relationship of halfmoon (*Medialuna californiensis*) based on 449 specimens.

Table 1. Sample size (N), mean standard length (mm SL), von Bertalanffy estimate of SL of each age class of opaleye. Age-0, 1, and 2 were determined by length frequency analysis (Pauly and David 1981).

Age Class	N	Mean SL	Estimated SL
0	190	57.6	59.7
1	19	150.0	147.1
2	7	201.3	199.1
3	21	234.1	230.0
4	43	245.0	248.3
5	16	251.1	259.2
6	15	248.7	265.7
7	5	273.2	269.6
8	2	289.5	271.8
9	1	273.0	273.2
10	2	280.0	274.0

Again, otolith weight was found to predict halfmoon age ($R^2 = 0.54$, $P < 0.001$). Sample sizes of each age class varied with age classes one and two containing the largest percent of halfmoon collected at 51% (Table 2).

The von Bertalanffy growth curves were highly asymptotic for both opaleye and halfmoon (Figures 5, 6). As demonstrated by these growth curves, the fastest growth rate of opaleye occurred from age zero to four when fish attained 90% of L_∞. This corresponds to growth rates of 92.4 mmSL/yr from Age-0 to Age-I opaleye, followed by 51.3 mm/yr for Age-I to II, 32.8 mm/yr for Age-II to III, and finally 10.9 mm/yr for Age-III to IV. Likewise, halfmoon grew fastest from age zero to three when fish attained 83% of L_∞ was attained. Corresponding growth rates for young halfmoon were 56.1 mm/yr from Age-0 to Age-I individuals followed by 11.7 mm/yr for Age-I to II, and 5.9 mm/yr for Age-II to III. Von Bertalanffy parameters for standard length growth curves for opaleye and halfmoon are presented in Table 3.

Discussion

Length-weight relationships determined by this study for both opaleye and halfmoon compared favorably with those listed by Quast (1968). His relationship for both sexes of opaleye ($W = 0.00005SL^{2.93}$), although similar was based on only 11 specimens. Likewise, the published relationship for both sexes of halfmoon ($W = 0.000008SL^{3.26}$) was similar, but based on only 10 specimens.

The asymptotic slope of the von Bertalanffy growth curve fit to standard length for both opaleye and halfmoon is typical of most herbivorous fishes (Choat and Robertson 2002). The fastest growth rates of opaleye and halfmoon occurred prior to sexual maturity at ages five and two, respectively (Fitch and Lavenberg 1971, 1975) after which growth in length slowed dramatically. This pattern of slowed somatic growth is common as fish redirect energy into reproduction after sexual maturity (Siems and Sikes 1998). This dominance of certain age classes is most likely a result of a sampling bias where as a large percentage of specimens were either juveniles from tidepools (as in opaleye) or caught as bycatch from gill nets with a mesh size of 2.5–5.1 cm and set at 5–14 m depth. This gill net bias probably also accounts for the relatively low L_∞ calculated for both species compared to the maximum recorded sizes. Love (1996) listed the maximum size of opaleye at 660 mm TL (541 mm SL) that is almost double of that determined herein (L_∞ = 275 mm SL). The maximum size (483 mm TL or 390 mm SL) for halfmoon (Love

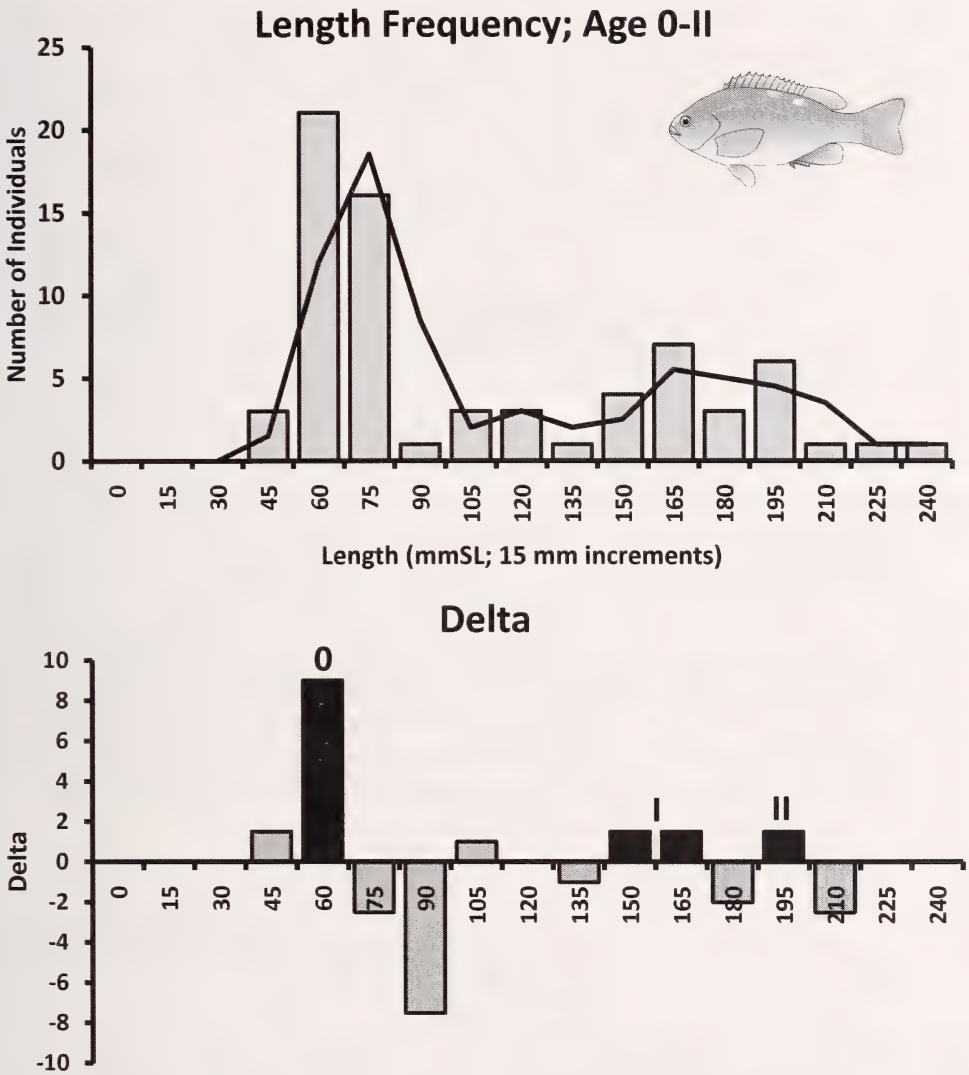

Fig. 4. Age class determination of Age-0, I, and II opaleye (*Girella nigricans*) (mm SL) determined by length frequency analysis as described in Pauly and David (1981). Top: Length frequency and moving, two-point average by 15 mm increments. Bottom: age class designation for 0, I, and II based on highest positive delta between frequency and moving two-point average.

1996) is closer than the L_∞ =284 mm SL determined in this study because the largest halfmoons in this study were collected using hook and line sampling. We can only conclude that large fish are out there, but are rarely caught in scientific gill nets.

Age and growth studies on kyphosids are rare in the literature; however, one study indicates opaleye and halfmoon have a similar life span to another temperate kyphosid. Pollock (1981) used scales to age luderick (*Girella tricsupidata*), a temperate, herbivorous fish found in the nearshore waters of Australia, at a maximum age of 11 years. Although similar to another kyphosid, the life-spans of both opaleye and halfmoon seem short when compared to similar sized temperate herbivorous acanthurids (surgeonfish) and scarids (parrotfish), in which most fishes reached a maximum age of over 20 years (Choat

Table 2. Sample size (N), mean standard length (mmSL), von Bertalanffy estimate of SL, mean weight (Wt in grams) and von Bertalanffy estimate of Wt (g) of each age class of halfmoon.

Age Class	N	Mean SL	Est. SL
0	17	26.0	34.4
1	45	185.5	160.3
2	44	218.8	222.8
3	18	235.6	253.8
4	8	247.9	269.2
5	2	272.5	276.8
6	1	297.0	280.6
7	0	-	282.5
8	2	297.5	283.4

and Robertson 2002). Similarly, age estimates of a central California herbivorous fish, monkeyface prickleback (*Cebidichthys violaceus*), are much higher than opaleye and halfmoon with a maximum age of 18 years (Marshall and Echeverria 1991).

Understanding life history attributes is important to evaluating the position of fishes in ecosystem food webs and their role in ecosystem processes. The results of this study indicate opaleye and halfmoon are relatively short-lived, fast growing fishes. The growth characteristics of opaleye and halfmoon coupled with their high abundance and productivity (Bredvik 2008, Boerger unpub. data) indicate that these herbivorous fishes may greatly influence the flow of energy in kelp forest ecosystems and their trophic role should be closely examined in future management of kelp forest communities (Adams 1980, King and McFarlane 2003, Depczynski et al. 2007, Leslie and McLeod 2007).

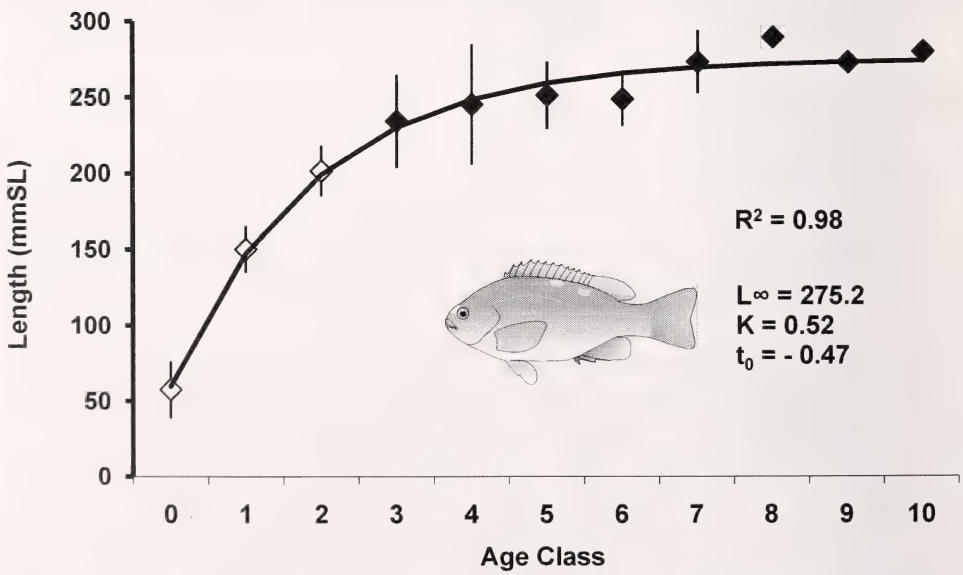

Fig. 5. Von Bertalanffy growth curve , R^2, $L\infty$, K, t_0 values for opaleye (*Girella nigricans*) fitted to standard length (mm, mean ± std) at age for all fish combined. Age-0, I, and II were determined by length frequency analysis (Pauly and David 1981).

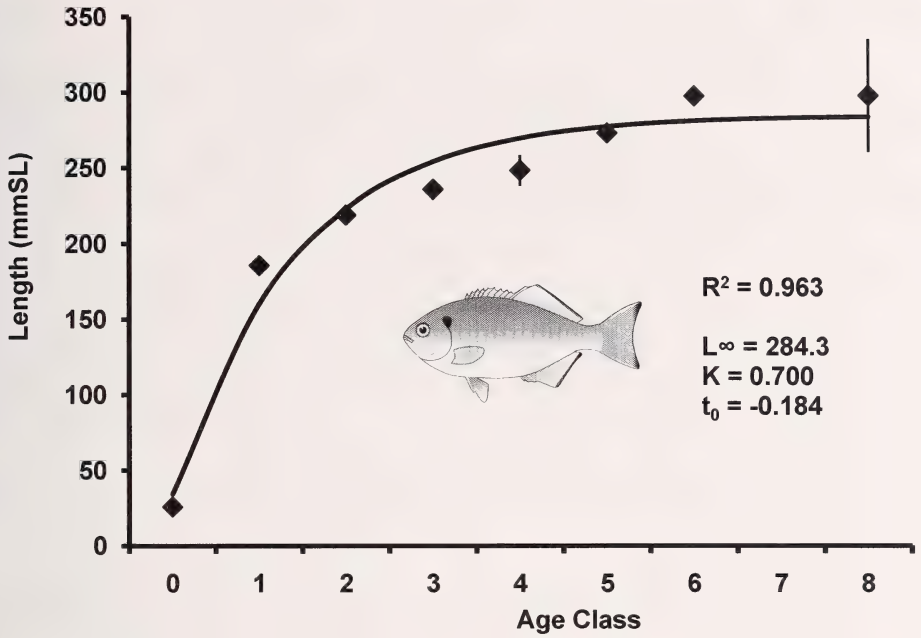

Fig. 6. Von Bertalanffy growth curves, R^2, $L\infty$, K, t_0 values for halfmoon (*Medialuna californiensis*) fitted to fitted to standard length (mm, mean ± std) at age for all fish combined.

Table 3. Growth parameters of opaleye and halfmoon for the von Bertalanffy model.

	Standard Length	
	Opaleye	Halfmoon
L_∞	275.2 mm	284.4 mm
K	0.52	0.70
t_0	−0.47 yr	−0.18 yr

Acknowledgments

We thank R. Carpenter, M. Franklin, D. Pondella, and M. Steele for helpful comments on early drafts of this manuscript and throughout this research project. This research was also aided by the members of the CSUN fish lab. The crew of the California State University's *R/V Yellowfin* namely Jim Cvitanovich, Dennis Maffey, and Dan Warren, worked tirelessly during each demanding gill net sampling period. Funding for this work was provided by CSUN Graduate Research and International Programs and under contract from the California Department of Fish and Game through the Ocean Resource Enhancement and Hatchery Program. Special thanks also to the staff at USC's Wrigley Marine Science Center, without which this research would not have been possible. All collecting and handling of the animals followed CSUN's animal care protocol and fish were collected under a California Fish and Game Scientific Collection Permit, # SC-000032.

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